



# Effects of stand composition and tree size on resistance and resilience to drought in sessile oak and Scots pine



Morgane Merlin\*, Thomas Perot, Sandrine Perret, Nathalie Korboulewsky, Patrick Vallet

Irstea, UR EFNO Ecosystèmes Forestiers, Centre de Nogent-sur-Vernisson, F-45290 Nogent-sur-Vernisson, France

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## ABSTRACT

The IPCC previsions for the upcoming decades include an increase in frequency and intensity of drought events in several regions worldwide, including Northern Europe. Drought significantly affects forest ecosystems through decreased productivity, increased vulnerability to biotic disturbances and increased subsequent mortality. How forest ecosystems maintain resistance and resilience to drought events are important questions. Our study aimed to assess whether species mixture or an individual tree size within a stand alters a given tree's resilience and resistance to drought. A retrospective study of tree-ring widths allowed us to calculate resistance, resilience and recovery indices for five recent drought events: 1976, the 1990–1992 period, 2003, 2006 and 2010. These drought events were selected based on the SPEI (Standardized Precipitation Evapotranspiration Index) drought index. Our study sample consisted of 108 individual sessile oak (*Quercus petraea* (Matt.)) or Scots pine (*Pinus sylvestris* L.) trees sampled in 2012 and 2013 (Orleans forest, central France) in pure and mixed stands, divided into three diameter classes corresponding to three sizes: large, medium and small trees. Scots pine performed better than sessile oak during the 1990–1992 and 2010 droughts while the contrary was observed for the 2003 and 2006 droughts. They performed equally in 1976. We suggest that the differing sensitivity of the two species to spring and summer drought explained this result. In our study, stand composition had no effect on resilience or resistance for either species. The size effect in oaks was unclear as small oaks displayed either a better performance or a worse performance than large oaks. Small pines displayed better resistance and resilience than pines of a larger size. This work stressed the importance of taking into account stand composition and trees size as well as soil and climatic conditions for each drought events to achieve a better understanding of the diversity of responses to climatic variations among forest ecosystems.

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## 1. Introduction

In the recent decades, the long term increase in temperature and changes in precipitation patterns (IPCC, 2013) accompanied by an increase in the frequency and intensity of extreme climatic events such as droughts (Smith, 2011) have been the object of several studies. The events are major disturbances, both ecologically and socially. The intense 1976 and 2003 droughts in Europe marked people's minds, and foresters were no exception. They were the first to witness forest decline and tree mortality following these droughts. The ability of forest ecosystems to face such climate changes and extreme events has become a major question for the scientific community. There is a large number of studies addressing this question (Bréda et al., 2006; Allen et al., 2010; Lloret et al., 2012). At the ecosystem level, the composition

(Smith, 2011; Cavin et al., 2013), structure and distribution of forests as well as the water, carbon and nutrient cycles are expected to be modified in the context of climate change (Bréda et al., 2006; Galiano et al., 2011; Cheaib et al., 2012). Impacts on tree growth and wood production are becoming significant with increasing forest decline and mortality in some parts of Europe, especially in Mediterranean environments (Martinez-Vilalta and Piñol, 2002; Vacchiano et al., 2012; Vilà-Cabrera et al., 2013).

To assess ecosystem stability or species response, three basic aspects can be considered: resistance, recovery and resilience (Grimm and Wissel, 1997). Resistance is the capacity of an ecosystem, species or individual to remain basically unchanged when it is subjected to a disturbance. Recovery is the capacity to regain growth or any other characteristic negatively affected after a disturbance. Resilience is the ability to recover pre-disturbance structures and functions after a disturbance. In the perspective of climate change, these three aspects are essential to conserving ecosystems and their functions, or at a smaller scale, species and even individuals.

\* Corresponding author.

E-mail address: [morgane.merlin@orange.fr](mailto:morgane.merlin@orange.fr) (M. Merlin).

Ecosystems involve several levels of complexity and diversity. Many studies have examined the benefits of mixed forests (Forrester et al., 2006; Kelty, 2006). Interest in mixed stands is inspired by observations of increased biodiversity in the ecosystem (Felton et al., 2010), better resistance to some biotic disturbances (Jactel and Brockerhoff, 2007; Perot et al., 2013) and an increase in productivity in most cases when compared to monoculture stands (Knoke et al., 2008; Vallet and Perot, 2011; Toigo et al., in press). Despite an increasing number of studies relative to mixed stands, we still know little about their functioning compared with pure stands. Niche complementarity, which enables a better use of the available resources – including water, is a common hypothesis to explain increased productivity in mixtures (Lebourgeois et al., 2013). Therefore, studying the potential consequences of climate change – induced modifications in water availability on mixed and monoculture stands is crucial. Two hypotheses could be made for the response of mixed stands to drought. Firstly, mixed stands could improve individual tree species' performance during drought; a species might be mixed with another species which does not occupy the same water reserves. This would lead to a release of intraspecific competition combined with the possibility of facilitation alleviating drought stress through a partitioning of the water reserves between the species (Lebourgeois et al., 2013; Pretzsch et al., 2013). The involved species would be expected to benefit from this interaction. Secondly and reversely, mixed stands could decrease individual species' performance during drought as it has been observed depending on the tree species and soil conditions. This would result in an increased interspecific competition during drought stress (Jucker et al., 2014). The involved species or the least competitive species would then suffer from mixing during water shortage periods, affecting tree growth and functions such as photosynthesis, transpiration or sap flow (Grossiord et al., 2014).

Another level of complexity in forest ecosystems lies in the existence of varying individual tree size within a stand. The majority of studies conducted on the impact of drought on forest stands focus on dominant trees, i.e. the largest in diameter with generally more developed crowns and root systems. It is possible to hierarchically organize the trees in an even-aged stand according to their diameter, reflecting differences between individual tree functional statuses within an even-aged stand (Dhôte, 1994). This hierarchy implies a differential availability of resources such as water (Dawson, 1996), nutrients and light (Dhôte, 1994). It also affects the intensity of competition between individuals. Population hierarchy can consequently play an important role in an individual's responses to climatic and biological disturbances (Pichler and Oberhuber, 2007; Martín-Benito et al., 2008; Mérian and Lebourgeois, 2011; Zang et al., 2012). It is important to incorporate both stand composition (pure or mixed stands) and individual tree size in the stand as explanatory variables when studying tree species response to abiotic disturbances such as drought in order to assess the risks associated with climate change and to propose adapted forest management strategies.

We studied the effects of tree size and stand composition on resistance and resilience to drought in terms of radial growth for two species: a deciduous broadleaved species; sessile oak (*Quercus petraea* Matt.) and a conifer needled species; Scots pine (*Pinus sylvestris* L.). These two tree species have very different characteristics, suggesting they may have different responses to drought (Bréda et al., 2006; Eilmann et al., 2006; Bréda and Badeau, 2008; Michelot et al., 2012a), and are widespread throughout European forests in both pure and mixed stands. Sessile oak is a mesophilic species with a deep root system which prefers semi-shady environments well adapted to occasional droughts. During periods of water deficit, leaf water potential is reduced, potentially leading to xylem cavitation. The large vessels in oak earlywood are very

sensitive to winter embolism (Tyree and Cochard, 1996) and water circulation must be restored each spring by the formation of at least one new tangential row of large vessels. Sessile oak is common in Western Europe and is the most widespread species in French forests (National Forest Inventory data). Scots pine is a light-demanding evergreen species. Its root system is more superficial than most broadleaved species but it does develop a strong first pivot and lateral roots. Water potential in the needles is maintained above a threshold level thanks to stomatal closure during periods of water deficit which minimizes the risk of xylem cavitation. Scots pine can stop its radial growth entirely when conditions are too harsh possibly leading to missing tree rings. Its drought tolerance as defined by Niinemets and Valladares (2006) is slightly higher than sessile oak. It is widely distributed throughout temperate and boreal Europe and is common in French forests and around the Mediterranean basin. Both species are present in pure or mixed stands at our study site in the Orléans National Forest in central France.

Radial growth is sensitive to biotic and abiotic disturbances (Lebourgeois et al., 2010; Olivar et al., 2012; Wiley et al., 2013; Palacio et al., 2014). It can be used for past climatic reconstructions or for retrospective analysis of tree performance during past known disturbances (Speer, 2010). We thus used radial growth to evaluate how individual trees responded to past climatic severe events such as drought using indices of resistance, recovery and resilience. We selected five drought events between 1970 and 2013 based on the SPEI (Standardized Precipitation Evapotranspiration Index), a drought index defined by Vicente-Serrano et al. (2010). We sought to answer the following three questions:

1. Do sessile oak and Scots pine respond differently to past drought events?
2. Does stand composition (mixed stand *versus* pure stand) improve or deteriorate individual tree's radial growth during drought events?
3. Does tree status represented by tree size affect individual tree's response to drought?

## 2. Material and methods

### 2.1. Study site and species

The study site is located in the center of France, in the Orléans National Forest (France, 48°00' N, 2°09' E) which extends over 35,000 hectares and is managed by the National Forest Office. Elevation ranges from 107 m to 174 m a.s.l. Throughout the forest the soil is relatively poor and acidic with a sandy clay-loam texture (Table 1), and is classified as a planosol (IUSS Working Group, 2014). Superimposed layers of clay and sand lead to a temporary perched water table in winter, but the low soil water storage capacity reduces available water for plants in summer. The area has a temperate continental climate with an oceanic influence (mean minimum temperature of 0.7 °C in February; mean maximum temperature of 25 °C in July). The mean annual rainfall is 740 mm (1969–2013 data from the weather station at Nogent-sur-Vernisson, France).

The species studied were sessile oak *Quercus petraea* (Matt.) and Scots pine *Pinus sylvestris* L., managed in pure or mixed stands.

### 2.2. Sampling design

Nine plots were selected on three sites in even-aged stands (50–80 years old) as part of the Oak Pine Tree Mixture Experiment (OPTMix) (Korboulewsky et al., 2013). Each site has one plot of pure sessile oak, one plot of pure Scots pine and one plot with a mixture of the two species. All plots have similar soil conditions,

**Table 1**  
Physico-chemical characteristics of the forest site soil (at 20–40 cm in depth, mean, standard deviation (s.d.),  $n = 30$ ). Cation exchange capacity (CEC) is given in milli-equivalents of hydrogen per 100 g (meq/100 g).

	Clay (%)	Fine silt (%)	Coarse silt (%)	Fine sand (%)	Coarse sand (%)	C (%)	N (%)	C/N	pH-KCl	CEC (meq/100 g)
Mean	8.6	11.8	7.9	14.3	55.8	0.92	0.046	19.6	4.43	4.21
(s.d.)	(2.4)	(2.8)	(2.3)	(2.2)	(7.5)	(0.25)	(0.010)	(2.9)	(0.16)	(2.58)

floral compositions, tree age, silvicultural treatments and diameter distributions (Table 2). For each plot, a 1.5–2 ha area was delimited and the position of each tree was mapped before the individual tree selection process. Nine trees per species and per plot were chosen according to a stratified sampling design with constraints. We studied the following two factors:

- The local composition or mixing rate: the mixing rate in the local environment (a 10 m-radius circle around each selected tree) was calculated as a percentage of the partial Relative Density Index, or RDI (Reineke, 1933). The calibration for both species of the self-thinning boundaries needed for the RDI calculation followed Charru et al. (2012) based on data from the National Forest Inventory for the northern half of France. In pure stands, the RDI proportion of the target species was 100%. In mixed stands, the RDI of the companion species was set between 40% and 80% to ensure that the sampled trees from pure and mixed stands had contrasted mixing rates.
- Tree size: this reflects the hierarchy in tree diameter between individual trees, related to the social status within the stand. We distinguished three tree size classes in our study: small trees, medium trees and large trees. Based on 2012 or 2013 tree diameters, the trees at each site were assigned to one of these classes. Understorey trees were excluded. For the selection process, we defined four quantiles from the diameter distribution for each species: 28% quantile, 38% quantile, 61% quantile and 71% quantile to obtain three intervals clearly separated. Small trees of a given species were sampled in the interval [minimum diameter; 28% quantile], medium trees were sampled in the interval [38% quantile; 61% quantile] and large trees were sampled in the interval [71% quantile; maximum diameter]. However, individual tree-level dynamics may have changed during the growing process due to modifications in the local environment or to genetics, and tree size may also have changed. To refine the influence of the hierarchy on the individuals' responses to each drought event, we redefined the tree size classes for each drought event studied here (see Section 2.4 for the selection of the drought events) based on three relative diameter classes (smallest, intermediate, largest) reconstructed from tree ring analyses.

The local density was estimated using the RDI. It was set between 0.5 and 0.75 to ensure similar competition conditions among sample trees. We visually checked the general form of the candidate trees to ensure that the selected trees were representative of the stand population.

The final sample consisted of 108 trees from the two species, the two stand composition types (pure or mixed) and the three tree size classes; three tree replicates per plot were included (Table 2). In autumn 2012 and 2013, the selected trees were felled and a 10 cm thick cross section was cut 1.30 m above the ground, or as close as possible to this level when defects (branches, damage or sap pockets) were present.

### 2.3. Tree-ring analyses

We used the WinDendro software (Regent, 2005) to measure tree-ring widths from pith to bark along two radii along a systematic north–south axis. The east–west axis was not used to avoid reaction wood or possible ovalization related to the prevailing east–west winds in this region. A visual crossdating was performed for known reference dates: – the 1976 drought and the *Diprion pini* attack on pine between 1981 and 1986 (Perot et al., 2013). We used a DigiMicro 2.0 Scale USB camera (Mikroskop Digital Kamera, DNT), an SMZ745 wen (Nikon) and an Eclipse E200 microscope (Nikon) to help us clarify the position of a few tree rings close to the pith. Statistical crossdating was performed with the COFECHA software (Grissino-Mayer, 2001).

The following statistics from the COFECHA software output (see Appendix B for detailed result for each sampled tree) were used to verify the quality of the tree-ring series (Grissino-Mayer, 2001). Series intercorrelation (SI) is a measure of the strength of the signal common to all the trees sampled. Most chronologies have values between 0.550 and 0.750. In our sample, SI was 0.577 for oak and 0.631 for pine. These values indicate a good common signal among the individuals sampled. The Expressed Population Signal (EPS) ensures that the trees sampled accurately represent a hypothetical population. This is verified when  $EPS > 0.85$  (Wigley et al., 1984). This condition was verified in our study with an EPS of 0.96 for sessile oak, and 0.98 for Scots pine.

The analysis was restricted to the 1970–2013 period, which corresponds to the extent of the meteorological data available for the study sites. Moreover, tree growth dynamics are usually different during the juvenile stage and the adult and mature stages. The choice of the 1970–2013 period ensured that the sampled trees were not in the juvenile stage (Fig. 2). Two radial growth variables were calculated. Ring width (RW) per year was calculated as the average ring width over the two radii along the north–south axis. Tree basal area increment (BAI) was calculated per year as follows:

$$BAI_n = (d_n^2 - d_{n-1}^2) \times \pi/4$$

**Table 2**  
Mean age and mean diameter at 1.30 m for each species, stand composition type and tree size class. The standard deviations for age and diameter are indicated in parentheses. Nine trees were sampled for each species, stand composition and size. S: small; M: medium; L: large.

Species	Sessile oak						Scots pine					
	Pure			Mixed			Pure			Mixed		
Size	S	M	L	S	M	L	S	M	L	S	M	L
Age (years)	63.0 (8.8)	65.6 (3.8)	65.9 (3.8)	65.1 (7.8)	68.7 (9.0)	72.0 (8.6)	55.0 (4.0)	56.0 (4.0)	56.2 (5.0)	57.6 (7.8)	61.8 (8.4)	68.0 (7.6)
Diameter (cm)	11.6 (1.5)	17.6 (1.9)	22.1 (2.2)	11.6 (1.8)	17.8 (2.4)	24 (3.6)	21.5 (2.0)	27.6 (1.1)	30.9 (3.1)	18.6 (2.8)	26.8 (1.1)	33.1 (2.8)

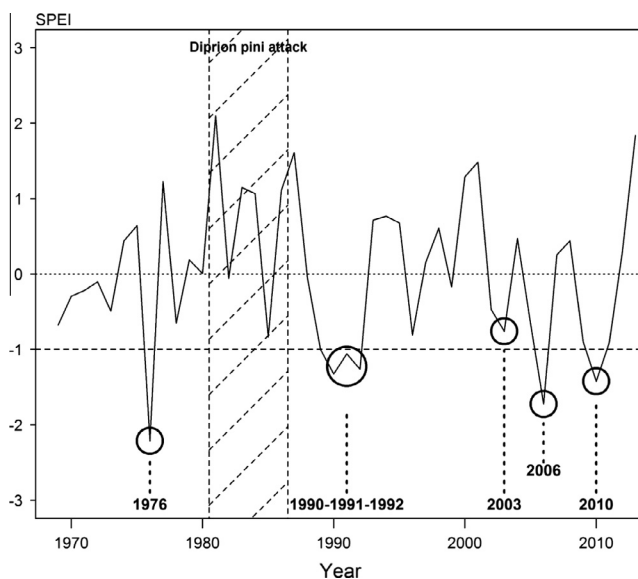
where  $d_n$  is tree diameter for year  $n$ .  $d_n$  was calculated from the cumulative ring widths of the tree ring series for each year.

#### 2.4. Climatic data and drought index

Daily minimum, maximum and average temperature and precipitation for the last 44 years (1969–2013) were collected from the Irstea weather station (France, 47°50' N, 2°44' E) located twenty kilometers from the study forest. Drought events were identified based on the SPEI (Standardized Precipitation Evapotranspiration Index) drought index (Vicente-Serrano et al., 2010) calculated with the *spei* CRAN package. This index has the advantage of incorporating the effects of temperature on drought and considering different time scales indicative of the chronic, long-term or exceptional character of each drought event and can be used to estimate changes in the dynamics and/or intensity of drought events over previous decades. Monthly SPEI is a standardized variable (see Vicente-Serrano et al. (2010) for details of the standardization). It is based on the degree of water surplus or deficit, defined as the difference between the monthly precipitation and the monthly Thornthwaite potential evapotranspiration (Thornthwaite, 1948). In this study, the SPEI for each year was calculated for the growing season spanning seven months from April to October. At this time scale, there is a fairly good correlation between the growth variables (RW for oak and BAI for pine, results not shown) and the SPEI values. When SPEI was under the value of -1, the year was considered a severe drought year (Potop et al., 2014). Following this criterion, the selected drought events in our study were: 1976, 2006, 2010 and the period 1990–1991–1992 (Fig. 1). We added the year 2003 since a short but intense summer drought event occurred then that has been largely studied as an important drought event in Europe (Ciais et al., 2005; Pichler and Oberhuber, 2007; van der Werf et al., 2007; Lebourgeois et al., 2010). Moreover, the SPEI during the summer months of 2003 was considerably below the threshold of -1, with a value of -2.4.

#### 2.5. Resistance, recovery and resilience indices

We used the resistance, recovery and resilience indices defined by Lloret et al. (2011) to quantify individual tree responses to the



**Fig. 1.** SPEI computed for the growing season (April to October) from 1970 to 2013. The selected drought events are indicated by a bold circle. The horizontal dotted line indicates the threshold of -1 below which a drought was considered severe. The 1981–1986 period (hatched zone) was removed from our analysis because of severe pine defoliation by *Diprion pini*.

drought events we selected. We hypothesized that pre-disturbance period reflect the expected growth missing during the year of the disturbance. To support this hypothesis, the growth variables on which the indices are based must not show any strong temporal trend, so we used RW for sessile oak and BAI for Scots pine (Fig. 2).

The absence of strong age-related trends (excluding the juvenile period) on these two growth variables allowed us to calculate the response indices with raw data (non-transformed or standardized data). Since comparing indices based on two different growth variables could be misleading when interpreting the species responses (see Section 2.6 for the statistical models), we quantified the error resulting from using BAI for Scots pine for each drought event. We included a multiplying factor  $R$  to link the index calculated with BAI with the one calculated with RW (see Appendix A for further details):

$$Index_{BAI} = Index_{RW} \times R$$

For the five drought events selected, the relative bias  $1 - R$  induced by the use of BAI for Scots pine is much smaller (around 4–9%) than the differences between the oak and pine responses (between 15% and 36%) for the same drought events (Appendix A, Fig. A1). The use of different growth indices for the two species does not influence the direction of the results obtained for the comparison of the two species (see Appendix A).

Growth during pre- and post-disturbance periods (*PreDr* and *PostDr*) was calculated as the average growth in the 3 years respectively before and after disturbance. There is a trade-off between retaining a long enough period to ensure a good estimation of the mean growth before and after the drought event and the risk of an overlap between the pre- or post-disturbance period and adjacent drought events. Growth during disturbance *Dr* is the growth observed the year of the drought event (or the average growth over the period of the disturbance in the case of a drought spanning several years, i.e. 1990 to 1992). Resistance, recovery and resilience are defined as follows (Fig. 3):

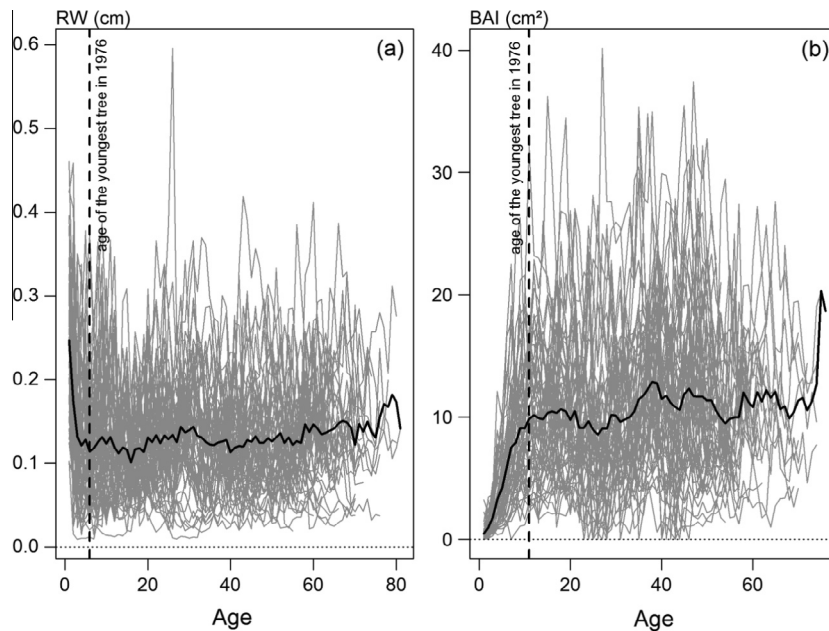
- Resistance =  $Dr/PreDr$ : the individuals' ability to withstand harsh conditions (e.g. drought).
- Recovery =  $PostDr/Dr$ : the individuals' ability to restore a level of growth after disturbance relative to the damage during the disturbance.
- Resilience =  $PostDr/PreDr$ : the ability of an individual to regain post-disturbance growth similar to pre-disturbance growth.

The post-disturbance period for 2003 and the pre-disturbance period for 2006 overlap. We therefore decided to use the 2006 post-disturbance period to calculate the 2003 indices and the 2003 pre-disturbance period for the 2006 indices. This choice removes the immediate impact on growth of the 2003 drought event on individual tree responses to the 2006 drought. It should also be noted that resilience for the 2010 drought event is incomplete for the trees sampled in 2012 as only two years of data were available after the drought event to calculate the resilience index for these trees.

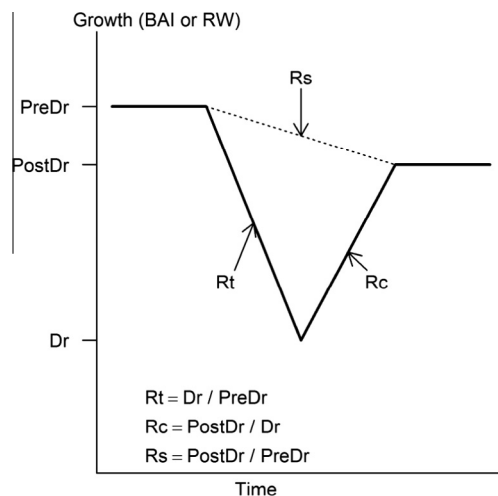
#### 2.6. Statistical analyses

Our first question on species specific response to drought was tested for each drought event. We used linear mixed models where response indices (transformed with the natural logarithm when necessary to meet the assumptions of normality of the residuals) were dependent variables and species (fixed factor) and plot (random factor) were explanatory variables. The linear mixed model for a given drought event was as follows, with sessile oak as the reference:





**Fig. 2.** Raw tree-ring growth series for sessile oak and Scots pine according to tree age. Each tree-ring series is printed in grey. The bold line represents the series mean averaged for all trees. (a) for sessile oak; the growth variable presented is RW, (b) for Scots pine: the growth variable presented is BAI. The vertical dotted line indicates the age in 1976 (oldest drought studied here) of the youngest tree sampled.



**Fig. 3.** Resistance  $R_t$ , recovery  $R_c$  and resilience  $R_s$  indices in a hypothetical case, adapted from Lloret et al. (2011). Resistance (solid line) and resilience (dotted line) correspond to the negative slopes, so the steeper the decline, the lower the resistance and resilience. Recovery (solid line) corresponds to the positive slope.

$$I_{ijk} = m + m_i + E_j + \varepsilon_{ijk}$$

where  $I_{ijk}$  is one of the three indices calculated for a tree  $k$  of a species  $j$  in plot  $i$ ,  $m$  is the intercept representing the sessile oak average for the relevant index and year;  $m_i$  is the plot random effect;  $E_j$  is the species effect (i.e. the difference for the relevant index and year between Scots pine and the reference – sessile oak) and  $\varepsilon_{ijk}$  are the residuals of the model. For each drought event, the species effect was removed in the model if it was found to be not significant.

We also used linear mixed models to answer our second and third questions on stand composition and tree size effects on individual's performance during drought events for each species and each drought event. The dependent variables were the indices of response to drought (log-transformed when necessary). The explanatory variables were stand composition (mixed or pure,

fixed effect), tree size (large, medium and small, fixed effect) and plot (random effect). The full linear mixed model used to test the effects of composition and tree size for a given drought event and one species was as follows, with large trees growing in pure stands as the reference:

$$I_{ijkl} = m + m_i + C_j + S_k + CS_{jk} + \varepsilon_{ijkl}$$

where  $I_{ijkl}$  is one of the three indices calculated for a tree  $l$  belonging to a size  $k$  in composition  $j$  for the plot  $i$ ,  $m$  is the intercept representing the reference (large trees growing in pure stands) average for the relevant index and year;  $m_i$  is the plot random effect;  $C$  is the composition effect (i.e. the difference between the reference – pure – and mixed stands);  $S$  corresponds to the tree size parameter (i.e. the difference between the reference – large – and each of the other two size classes);  $CS$  is the interaction between composition and size; and  $\varepsilon_{ijkl}$  are the residuals of the model. For each model, variables which were found to be not significant were removed to improve the estimations of the significant variables. The interaction parameter  $CS$  was consequently removed from all models as it was never significant. All statistical analyses were performed with the *nlme* package of the R statistical software (R Development Core Team, 2014). The significance threshold was set at 0.05.

### 3. Results

Growth decreased during the drought events for both sessile oak and Scots pine as resistance values were less than 1 in average

**Table 3**

Mean values (and standard deviation s.d.) of the resistance, recovery and resilience indices. Mean values are calculated for each species over the five selected drought events.

	Resistance $R_t$		Recovery $R_c$		Resilience $R_s$	
	Oak	Pine	Oak	Pine	Oak	Pine
Mean	0.759	0.787	1.361	1.366	0.994	0.985
s.d.	0.218	0.274	0.606	0.765	0.434	0.457

**Table 4**

Results from the linear mixed models for species effect on resistance Rt, recovery Rc and resilience Rs indices for the five selected drought events. For each model, when the “species” variable was not significant, we chose to remove it completely. Parameters are estimated with sessile oak as the reference. *ln* below a drought event indicates that logarithm transformation of the response variable was used to fit the model. The estimates and standard deviations (s.d.) were not back transformed when the logarithm was applied. Significant results are shown in bold characters. Shading indicates the direction of the difference between Scots pine and the reference, i.e. sessile oak; dark grey: positive difference; light grey: negative difference.

		1976	1990–1992	2003	2006	2010
Rt	Intercept		<i>ln</i>		<i>ln</i>	<i>ln</i>
	Estimation	<b>0.668</b>	<b>–0.405</b>	<b>0.951</b>	<b>–0.307</b>	<b>–0.305</b>
	s.d.	<b>0.018</b>	<b>0.038</b>	<b>0.034</b>	<b>0.057</b>	<b>0.043</b>
Scots pine	p-value	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
	Estimation		<b>0.257</b>	<b>–0.155</b>	<b>–0.345</b>	<b>0.275</b>
	s.d.		<b>0.054</b>	<b>0.041</b>	<b>0.066</b>	<b>0.051</b>
Rc	p-value		<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
	Estimation	<i>ln</i>	<i>ln</i>	<i>ln</i>	<i>ln</i>	<i>ln</i>
	s.d.	<b>0.514</b>	<b>0.336</b>	<b>0.123</b>	<b>0.320</b>	<b>–0.272</b>
Scots pine	p-value	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>0.002</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
	Estimation				<b>0.235</b>	<b>–0.172</b>
	s.d.				<b>0.059</b>	<b>0.051</b>
Rs	p-value				<b>&lt;0.001</b>	<b>&lt;0.001</b>
	Intercept	<i>ln</i>	<i>ln</i>	<i>ln</i>	<i>ln</i>	<i>ln</i>
	Estimation	<b>0.087</b>	<b>–0.091</b>	<b>–0.046</b>	<b>–0.046</b>	<b>–0.526</b>
Scots pine	s.d.	<b>0.056</b>	<b>0.061</b>	<b>0.038</b>	<b>0.038</b>	<b>0.076</b>
	p-value	<b>0.126</b>	<b>0.134</b>	<b>0.236</b>	<b>0.236</b>	<b>&lt;0.001</b>
	Estimation		<b>0.287</b>			
	s.d.		<b>0.074</b>			
	p-value		<b>&lt;0.001</b>			

**Table 5**

Results from the linear mixed models for stand composition and tree size effects on resistance Rt, recovery Rc and resilience Rs indices of sessile oak for the five selected drought events. Parameters are estimated with pure stands and large trees as the references. *ln* below a drought event indicates that logarithm transformation of the response variable was used to fit the model. Estimates and standard deviations (s.d.) were not back transformed when the logarithm was applied. Significant results are shown in bold characters. Shading indicates the direction of the difference between each factor level and the references, i.e. large trees and pure stands; dark grey: positive difference; light grey: negative difference.

			1976	1990–1992	2003	2006	2010
Rt	Intercept	Estimates	<b>0.654</b>	<i>ln</i> <b>–0.537</b>	<b>1.041</b>	<b>0.732</b>	<i>ln</i> <b>–0.304</b>
		s.d.	<b>0.022</b>	<b>0.059</b>	<b>0.063</b>	<b>0.023</b>	<b>0.062</b>
		p-value	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
Composition	<i>Mixed</i>	Estimates					
		s.d.					
		p-value					
Size	<i>Medium</i>	Estimates		<b>0.155</b>	<b>–0.121</b>		
		s.d.		<b>0.071</b>	<b>0.063</b>		
		p-value		<b>0.034</b>	<b>0.059</b>		
	<i>Small</i>	Estimates		<b>0.241</b>	<b>–0.130</b>		
		s.d.		<b>0.071</b>	<b>0.063</b>		
		p-value		<b>0.001</b>	<b>0.043</b>		
Rc	Intercept	Estimates	<i>ln</i> <b>0.624</b>	<b>1.443</b>	<i>ln</i> 0.086	<b>1.572</b>	<b>0.850</b>
		s.d.	<b>0.090</b>	<b>0.071</b>	0.062	<b>0.079</b>	<b>0.064</b>
		p-value	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.175	<b>&lt;0.001</b>	<b>&lt;0.001</b>
Composition	<i>Mixed</i>	Estimates					
		s.d.					
		p-value					
Size	<i>Medium</i>	Estimates				<b>–0.262</b>	<b>–0.068</b>
		s.d.				<b>0.090</b>	<b>0.043</b>
		p-value				<b>0.005</b>	<b>0.117</b>
	<i>Small</i>	Estimates				<b>–0.129</b>	<b>–0.125</b>
		s.d.				<b>0.090</b>	<b>0.043</b>
		p-value				<b>0.157</b>	<b>0.005</b>
Rs	Intercept	Estimates	<i>ln</i> 0.169	<i>ln</i> <b>–0.070</b>	<b>1.052</b>	<b>1.052</b>	<i>ln</i> <b>–0.573</b>
		s.d.	0.010	0.062	<b>0.063</b>	<b>0.063</b>	<b>0.106</b>
		p-value	0.098	0.271	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
Composition	<i>Mixed</i>	Estimates					
		s.d.					
		p-value					
Size	<i>Medium</i>	Estimates					
		s.d.					
		p-value					
	<i>Small</i>	Estimates					
		s.d.					
		p-value					

(Table 3). Mean index values showed relatively high levels of resistance to drought and resilience for both species (Table 3).

### 3.1. Comparison between the two species' response to drought events

The species effect was significant for some drought events, and differs depending on the index. Pine was more resistant than oak for 1990–1992 and 2010 droughts and more resilient for the 1990–1992 drought only. Oak was more resistant for the 2003 and 2006 droughts, recovered better after the 2010 drought (Table 4).

### 3.2. Effects of stand composition on species responses to drought events

The effect of stand composition (pure or mixed stands) on sessile oak or Scots pine responses was never significant for the selected drought events and was thus removed from all models (Tables 5 and 6).

### 3.3. Effects of tree size on species responses to drought events

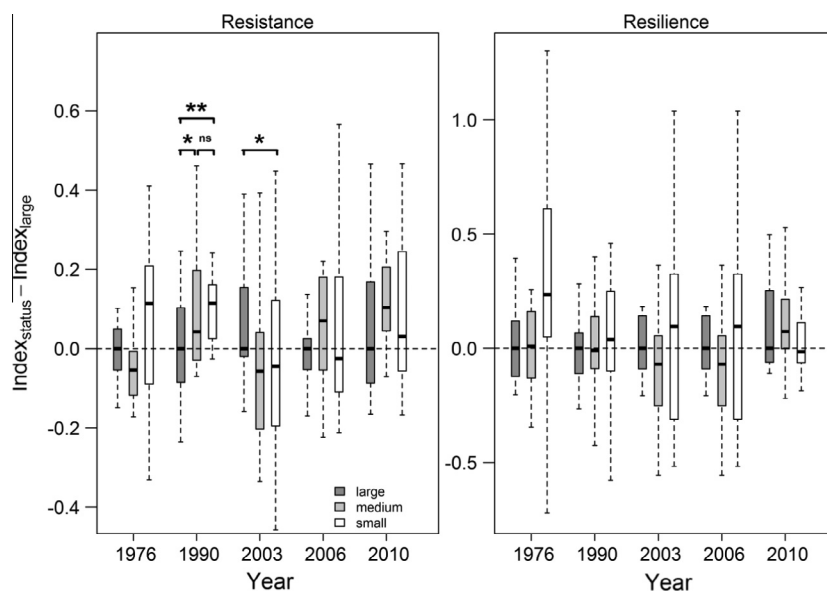
#### 3.3.1. Sessile oak

The effect of the tree size on the sessile oak response to drought was variable depending on the year and the index considered.

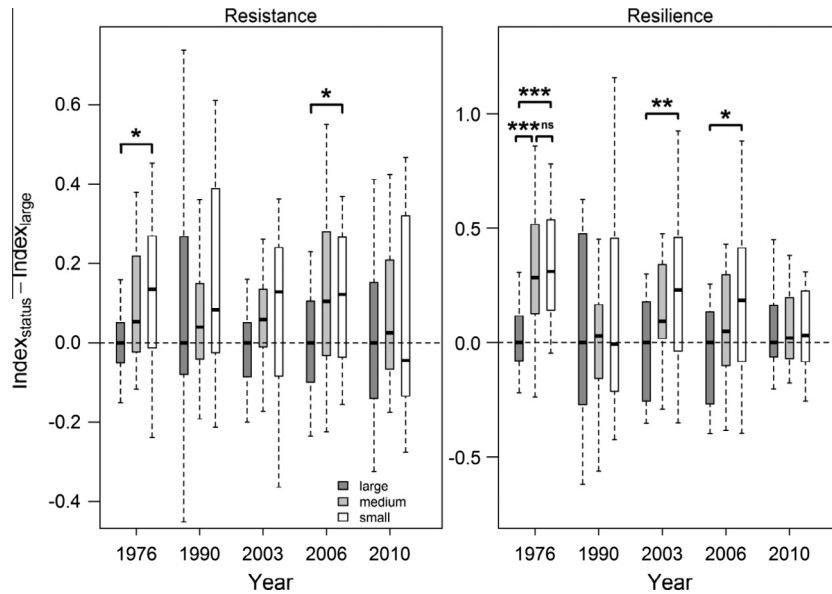
**Table 6**

Results from the linear mixed models for stand composition and tree size effects on resistance  $R_t$ , recovery  $R_c$  and resilience  $R_s$  indices of Scots pine for the five selected drought events. Parameters are estimated with pure stands and large trees as the references.  $\ln$  below a drought event indicates that logarithm transformation of the response variable was used to fit the model. Estimates and standard deviations (s.d.) were not back transformed when the logarithm was applied. Significant results are shown in bold characters. Shading indicates the direction of the difference between each factor level and the references, i.e. large trees and pure stands; dark grey: positive difference; light grey: negative difference.

			1976	1990–1992	2003	2006	2010
$R_t$	Intercept	Estimates	<b>0.607</b>	$\ln$ <b>–0.148</b>	<b>0.790</b>	<b>0.481</b>	$\ln$ <b>–0.029</b>
		s.d.	<b>0.045</b>	<b>0.058</b>	<b>0.022</b>	<b>0.059</b>	0.032
		p-value	<b>&lt;0.001</b>	<b>0.014</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.367
Composition	Mixed	Estimates					
		s.d.					
		p-value					
Size	Medium	Estimates	0.088			0.105	
		s.d.	0.052			0.065	
		p-value	0.095			0.112	
	Small	Estimates	<b>0.128</b>			<b>0.137</b>	
		s.d.	<b>0.052</b>			<b>0.065</b>	
		p-value	<b>0.017</b>			<b>0.041</b>	
$R_c$	Intercept	Estimates	$\ln$ <b>0.425</b>	$\ln$ <b>0.334</b>	<b>1.220</b>	<b>1.801</b>	$\ln$ <b>–0.450</b>
		s.d.	<b>0.085</b>	<b>0.044</b>	<b>0.058</b>	<b>0.126</b>	<b>0.091</b>
		p-value	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
Composition	Mixed	Estimates					
		s.d.					
		p-value					
Size	Medium	Estimates					
		s.d.					
		p-value					
	Small	Estimates					
		s.d.					
		p-value					
$R_s$	Intercept	Estimates	$\ln$ <b>–0.220</b>	$\ln$ <b>0.186</b>	$\ln$ <b>–0.288</b>	$\ln$ <b>–0.253</b>	$\ln$ <b>–0.479</b>
		s.d.	<b>0.070</b>	<b>0.092</b>	<b>0.080</b>	<b>0.081</b>	<b>0.100</b>
		p-value	<b>0.003</b>	<b>0.049</b>	<b>0.001</b>	<b>0.003</b>	<b>&lt;0.001</b>
Composition	Mixed	Estimates					
		s.d.					
		p-value					
Size	Medium	Estimates	<b>0.323</b>		0.219	0.149	
		s.d.	<b>0.089</b>		0.113	0.115	
		p-value	<b>&lt;0.001</b>		0.059	0.203	
	Small	Estimates	<b>0.337</b>		<b>0.310</b>	<b>0.275</b>	
		s.d.	<b>0.089</b>		<b>0.113</b>	<b>0.115</b>	
		p-value	<b>&lt;0.001</b>		<b>0.009</b>	<b>0.021</b>	



**Fig. 4.** Difference between the resistance or resilience index value for large sessile oak trees and the values for the other tree size classes for each drought event. For each year and tree size, the segments and stars indicate the level of significance of the difference between large Scots pine trees and other trees from the models. The models were re-run with the medium size as the reference to test the difference between this size and the small size. \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ ; ns: not significant.



**Fig. 5.** Difference between the resistance or resilience index value for large Scots pine trees and the values for the other tree size classes for each drought event. For each year and tree size, the segments and stars indicate the level of significance of the difference between large Scots pine trees and other trees from the models. The models were re-run with the medium size as the reference to test the difference between this size and the small size. \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ ; ns: not significant.

In 2003, 2006 and 2010, small trees showed significantly lower resistance (2003) or recovery (2006, 2010) than did large trees. The opposite result was found for resistance for the 1990–1992 drought event (Table 5 and Fig. 4). There was no effect of tree size on sessile oak resilience for any of the five drought events considered.

### 3.3.2. Scots pine

Several significant results were found. The general trend for Scots pine indicates better resistance and resilience among small individuals than among large individuals (Table 6 and Fig. 5). There were no significant effects of stand composition or tree size for some indices and drought events (Table 6).

## 4. Discussion

As expected, both species reduced their radial growth during drought events. When drought occurs, photosynthesis is reduced leading to less carbon available for functions such as radial growth which in turn decreases (Chaves et al., 2003; Palacio et al., 2014).

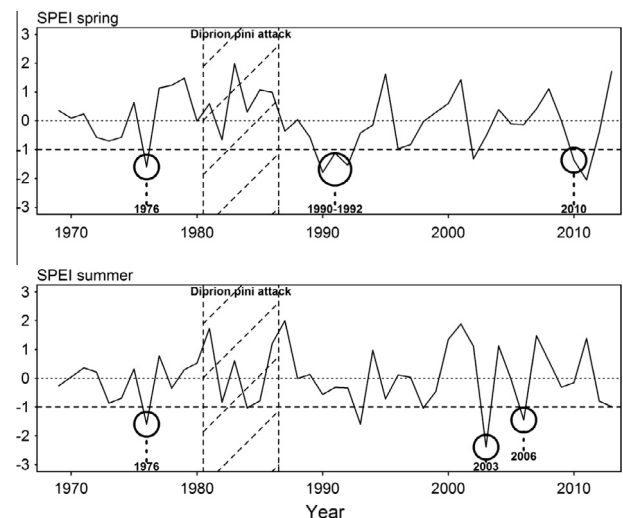
Resistance and resilience to drought differed between oak and pine, as expected (Table 4), though the mean values for each species were close to each other (Table 3). Stand composition had no effect on the resistance indices of the species studied (Tables 5 and 6). However, tree size did have an effect in some cases. The influence of tree size was pronounced and unidirectional for resistance and resilience in Scots pine for several drought events. Results for sessile oak show that the size effect varied between drought events or indices.

### 4.1. Oak and pine respond differently to drought events

We first showed that sessile oak and Scots pine responded differently to the five drought events studied. Pine was more resistant during the 1990–1992 drought period and the 2010 drought while oak was more resistant during the 2003 and 2006 droughts. The drought events studied here occurred at different periods during the growing season and this could have influenced the responses

of the two species. Indeed, several studies have shown that pine and oak species have different growth dynamics during the growing season (Weber et al., 2007; Eilmann et al., 2009; Michelot et al., 2012b). Complementary analyses of the SPEI over the spring (March to May) and summer months (June to August) separately revealed different types of drought (Fig. 6).

The 1976 drought was global throughout the whole growing season. The 1990–1992 and 2010 droughts occurred in the spring while the 2003 and 2006 droughts were intense summer droughts. Our results suggest that Scots pine was more resistant during spring droughts than sessile oak, and that sessile oak was more resistant during summer droughts (Table 4). The 1976 drought, which lasted through spring and summer, should



**Fig. 6.** SPEI computed for spring (April–June) and for summer (July–August) from 1970 to 2013. The selected drought events are indicated by a bold circle. The horizontal dotted line indicates the threshold of  $-1$  below which a drought was considered severe. The 1981–1986 period (hatched zone) was removed from our analysis because of severe pine defoliation by *Diprion pini*.



have affected both species; our results confirm this (we found no difference between the two species for any index, Table 4). Their differing growth dynamics, particularly how the two species form intra-annual wood, could explain this time-dependent resistance. Zweifel et al. (2006) showed that pubescent oak (*Quercus pubescens*) starts radial growth about one month before leaf expansion, achieving almost half of the annual radial increment by the time the leaves reach full expansion at the end of spring. Furthermore, oak species have been found to be more sensitive to spring conditions, and particularly to water availability during spring, than to summer conditions and droughts (van der Werf et al., 2007; Weber et al., 2007; Eilmann et al., 2009; Zang et al., 2012; Morán-López et al., 2014). Earlywood vessels in oak are formed before and during budburst using stored reserves from the previous growing season (Corcuera et al., 2004). These newly formed vessels are wide allowing such ring-porous species to transport more water during early growing season but at the expense of increased embolism risk. They rapidly become embolized as conditions become more stressful during the growing season (Cochard and Tyree, 1990). During spring droughts, the oak's newly formed vessels are exposed to the risk of cavitation leading to water deficit and reduced cell enlargement. Water stress during spring is thus the most important factor controlling radial growth for oak (Tardif and Conciatori, 2006). This phenomenon constrains ring width despite the potential activation of drought avoidance mechanisms (Eilmann et al., 2009). In contrast, summer drought would be of less consequence on oak radial growth as the radial increment would have mainly occurred during the months preceding the drought. However, a summer drought still reduces photosynthetic activity for oak through stomatal closure, which prevents further accumulation of reserves for the following year's growth (Chaves et al., 2003). For Scots pine, on the other hand, needles only appear during the summer and the tree has achieved a mere fourth of its annual radial increment by the time needles reach full expansion (Zweifel et al., 2006). This species' radial growth dynamics, which have been extensively studied in Europe, show a stronger dependency on conditions at the end of spring and during the summer months (Weber et al., 2007; Eilmann et al., 2009; Eilmann et al., 2011; Zang et al., 2012; Taeger et al., 2013). Spring droughts constrain pine growth and might lead to the cavitation of some xylem tracheids. However, pine can continue its radial growth when the conditions become better after the spring drought subsides, resulting in wider ring widths during spring drought years than for oak. Summer droughts, on the other hand, quite strongly affect pine growth because they hamper needle formation and reduce cell enlargement, consequently reducing the radial increment for that year, in contrast to oak.

Results for recovery were less pronounced than for resistance: for resistance, four out of five drought events showed significant differences between the two species while only two out of five drought events showed significant differences for recovery (Table 4). However, assuming that both resistance to and recovery from drought events depend on the amount of carbon reserves available, a compromise might be established between these two indices (Galiano et al., 2011; Lloret et al., 2011). As mentioned before, ring widths for oak show a strong relationship with climatic conditions of the previous year, even when the current year's conditions are favorable (Zweifel et al., 2006; van der Werf et al., 2007; Eilmann et al., 2009; Michelot et al., 2012b). A summer drought does not constrain oak ring width but does constrain its photosynthetic activity, thus reducing the amount of reserves stored for the establishment of the following year's tree ring. This was observed for 2004, following the 2003 drought, for some individuals in our study (data not shown) and for 2007, following the 2006 drought (van der Werf et al., 2007). The longer growing season for Scots

pine (Michelot et al., 2012b) as well as its ability to maintain photosynthesis throughout autumn and winter thanks to its evergreen leaves limit its dependence on the previous year's accumulated reserves for recovery after a drought event (Gruber et al., 2012). This compromise between resistance and recovery explains that in 2006 (summer drought) and 2010 (spring drought), we found opposite results for resistance and recovery (Table 4). However, this idea of a potential compromise between resistance and recovery based on the amount of carbon reserves available needs further investigation.

#### 4.2. Stand composition has no effect on resistance and resilience

Neither pine nor oak responses to the selected drought events depended on stand composition (pure or mixed) (Table 5). This result was unexpected as results in the literature usually present various effects of species mixtures in forests in case of biotic and abiotic disturbances, whether they present benefits or drawbacks (Knocke et al., 2008; Maestre et al., 2009; Felton et al., 2010; Lebourgeois et al., 2013; Perot et al., 2013; Pretzsch et al., 2013).

Assuming equivalent stand density, lower growth in mixed stands associated to drought episodes would indicate stronger between-species competition (Grossiord et al., 2014) than within-population competence. The absence of this pattern in our results indicates that drought conditions did not increase between-species competition, suggesting that water acquisition for each species was not disrupted by the presence of the other species. The absence of any benefits (higher growth) of the mixed stands also suggests the absence of any complementarity process (through root stratification for example e.g. Pretzsch et al. (2013)) in our study sites during drought, which might be related to the type of soil encountered in the study plots prohibiting deep root extension (Table 1).

Moreover, the trees sampled in this study had all necessarily survived the selected drought events. Trees which died during these drought events might have had an impact at the stand level on the stand composition effect. A long-term survey including mortality is needed to more precisely define the effects of stand composition on individuals' response to drought. Lastly, the stand composition effect might be reflected in structural characteristics other than ring widths. There is a growing number of studies focusing on other wood characteristics such as the relative widths of earlywood and latewood, the number and size of vessels, and ring density. These parameters would add a degree of precision to the understanding of the processes governing tree growth and cambial activity (Martínez-Vilalta and Piñol, 2002; Eilmann et al., 2009; Martín-Benito et al., 2013; Vieira et al., 2014).

#### 4.3. The tree size effect on individual tree response to drought varies between species

In *Pinus sylvestris* large trees were more sensitive than small trees to drought, while no clear trend was observed for *Quercus petraea* (Tables 5 and 6).

##### 4.3.1. Small oak response seems better for older droughts than for recent droughts

The results obtained for sessile oak show varying effects of tree size depending on the drought event and the index (Table 5, Fig. 4). We observed a better response of small trees for the 1990–1992 drought (resistance), and the opposite for the 2003 (resistance), and 2010 droughts (recovery) while medium-sized trees responded better in terms of recovery for the 2006 drought. Several hypotheses could be made to explain these results. As it has

been suggested before, the type of drought could play a major role in shaping trees' responses to such disturbances. The 1990–1992 drought and the 2003 drought have very different characteristics: the first one was a drought spanning several years and more related to water stress than temperature stress while the second one was very short and intense and more related to temperature stress. The 2003, 2006 and 2010 droughts were frequent, happening only a few years apart from each other while the 1990–1992 drought happened 15 years after the previous drought which was in 1976. Small and large trees could reasonably respond differently to these varying characteristics of droughts, explaining the results we observed in our study. Processes related to drought hardening for example in small trees as suggested by Martín-Benito et al. (2008) might confer them an advantage while large trees might recover faster in the favorable years following a drought (Martín-Benito et al., 2008; Martínez-Vilalta et al., 2012). Moreover, we could imagine that oaks could respond differently to droughts as they grow older (as suggested by Lloret et al. (2011) and Martínez-Vilalta et al. (2012) for pine species) leading to a potential change in the direction of the individual tree response to different drought effects, as we observed between the 1990–1992 drought and the following droughts. Unfortunately, very few references could be found and our results could not support one hypothesis more than another.

#### 4.3.2. Small pines' response to drought is better than large pines

The results for Scots pine are unambiguous: when tree size is significant, trees of lower size (e. g. medium or small) have better responses to drought than large trees in terms of resistance, and above all, resilience (Table 6 and Fig. 5). It can be noted that these differences are observed only for summer droughts (no tree size effect for the 1990–1992 and 2010 spring droughts). In our stands, the variability of Scots pine diameters is associated with a stratification of tree crowns (through different crown transparency and expansion). Thus, microsite climatic conditions (humidity, temperature or solar radiation) might be kept relatively favorable for small trees, providing them with better growing conditions despite the overall drought conditions (Aussenac, 2000). Small trees may also be drought-hardened due to their position in the stand. Their need for carbon, nutrients and water would thus be reduced while their efficiency to use these resources might be enhanced. These drought-hardening adaptations (Martín-Benito et al., 2008) as well as the micro-climatic conditions could enable the small trees to sustain growth while conditions are too harsh for large trees with high resource and maintenance needs as found in the literature (Martín-Benito et al., 2008; Martínez-Vilalta et al., 2012; Zang et al., 2012).

However, other results in the literature contradict our results, showing that small trees are more affected by drought events than large trees (Orwig and Abrams, 1997; Pichler and Oberhuber, 2007) due to a shallower root system or increased intraspecific competition (Martín-Benito et al., 2008; Zang et al., 2012), or no tree size effect at all (Mérian and Lebourgeois, 2011).

Variability in the definition and magnitude of the tree size classes analyzed and the indices used in other studies and in ours may play a role in these conflicting results. Different soil and climatic conditions at each study site can also modify the response thresholds of individual trees. Finally, our study shows that in the same environmental context, the tree size effect varies according to the species considered (Lebourgeois et al., 2014), though we have yet to provide an explanation for this variation. Nevertheless, it is important to take into account the tree size classes within a stand in the study of the responses to climatic and/or biotic disturbances, as some previous studies have noted (Orwig and Abrams, 1997; Martín-Benito et al., 2008; Mérian and Lebourgeois, 2011; Zang et al., 2012; Eilmann et al., 2013).

## 5. Conclusion

Our study confirms the differing responses of sessile oak and Scots pine to several specific drought events. Our results suggest that summer and spring droughts do not have the same impact on different species, though the limited number of drought events in our data did not enable us to test this hypothesis. The two species' contrasted growth dynamics and timing may lead to different consequences from a spring or a summer drought. Specific responses to different types of drought should be considered in future studies. Our results indicated no adverse or beneficial effects of mixture on the two species' resistance, resilience and recovery to drought. Tree size significantly affected both species, though the direction of this effect was not clear in sessile oak while it was for Scots pine, showing a better response of small trees to drought events. We hypothesize that intra-specific facilitation and/or physiological adaptations confer an advantage to small individuals during periods of water stress, though results from the literature are contradictory. The long-term monitoring of forest stands makes it possible to take into consideration mortality events following disturbances; a severe drought can speed up the mortality process for weak trees (Pedersen, 1998; Galiano et al., 2010) but less so for strongly growing trees. Such experiments are in progress in the research unit where the OPTMix experimental site is located. Our study provides support for good resilience among surviving individuals of sessile oak and Scots pine in this lowland forest, which is facing climate change and increased drought frequency. This research is essential to adapt forest management strategies to changing conditions, while taking economic requirements into account.

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## Appendices A and B. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2014.11.032>.

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